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Historical fire and vegetation dynamics in dry forests of the interior Pacific Northwest, USA, and relationships to Northern Spotted Owl (*Strix occidentalis* caurina) habitat conservation

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ABSTRACT

Regional conservation planning frequently relies on general assumptions about historical disturbance regimes to inform decisions about landscape restoration, reserve allocations, and landscape management. Spatially explicit simulations of landscape dynamics provide quantitative estimates of landscape structure and allow for the testing of alternative scenarios. We used a landscape fire succession model to estimate the historical range of variability of vegetation and fire in a dry forest landscape (size ca. 7900 km^2) where the present-day risk of high severity fire threatens the persistence of older closed canopy forest which may serve as Northern Spotted Owl (*Strix occidentalis* caurina) habitat. Our results indicated that historically, older forest may have comprised the largest percentage of the landscape (~35%), followed by early successional forest (~25%), with about 9% of the landscape in a closed canopy older forest condition. The amount and condition of older forest varied by potential vegetation type and land use allocation type. Vegetation successional stages had fine-grained spatial heterogeneity in patch characteristics, with older forest tending to have the largest patch sizes among the successional stages. Increasing fire severities posed a greater risk to Northern Spotted Owl habitat than increasing fire sizes or frequencies under historical fire regimes. Improved understanding of historical landscape-specific fire and vegetation conditions and their variability can assist forest managers to promote landscape resilience and increases of older forest, in dry forests with restricted amounts of habitat for sensitive species.

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1. Introduction

Regional forest planning efforts frequently address conservation issues in a context of limited information about the species, habitat, and temporal dynamics of the ecosystems under management. The Northwest Forest Plan (NWFP) established a static network of late successional reserves (LSRs) across western Washington, Oregon, and northern California (USA) to provide habitat for the Northern Spotted Owl (*Strix occidentalis* caurina; "NSO") and other older forest associates (U.S.D.A. Forest Service and U.S.D.I. Bureau of Land Management, 1994a,b). The NSO was listed in 1990 as threatened under the U.S. Endangered Species Act. NSO habitat is characterized by larger conifer trees, more conifer canopy closure, less deciduous canopy closure, and greater structural complexity than the landscape as a whole (Davis and Lint, 2005). Whereas most of the range of the NSO is in wet forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) (Franklin and Dyrness, 1988), 36% occurs in the drier forests of the eastern Cascade Mountains in Oregon and Washington, the California Cascades, and the Klamath Provinces of southern Oregon and Northern California. In these forests, desired conditions for NSO habitat include maintenance and restoration of semi-closed-to-closed canopy older forests (U.S. Fish and Wildlife Service, 2008).

However, the overall area and configuration of LSRs may be inadequate in these dry forests for the persistence and development of older forest structure in the amounts specified by the NWFP. Several challenges face NSO recovery there. At present, the dry forests have a large buildup of fuels (Agee, 2003a; Hessburg et al., 2005) and high risk of loss of older forest from high severity fire (Lee and Irwin, 2005; U.S. Fish and Wildlife Service, 2008). In the past decade, losses to wildfire have been substantial (Moeur et al., 2005). Recent large fires in the dry forests of Oregon's Klamath and East Cascades Provinces have been the subject of much research (Agee, 2003b; Donato et al., 2006; Stokstad, 2006;

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Ager et al., 2007; Campbell et al., 2007; Saab et al., 2007; Shatford et al., 2007; Thompson et al., 2007). In addition, the NSO faces other novel challenges such as the threat from the barred owl (*Strix varia*) and West Nile virus (*Flavivirus* sp.).

For the Cascades Provinces, recovery goals include identifying, maintaining and restoring high-quality habitat patches in habitat-capable areas; in the dry forest types these patches are to be spatially dynamic. However, knowledge of fire and vegetation dynamics that would promote reaching these goals in dry forests remains limited (Spies et al., 2006; U.S. Fish and Wildlife Service, 2008). In particular, more information is needed about the spatial and temporal patterns of historical reference conditions in these forests, and the spatial variability in risk of loss of older forest from fires. Achieving these goals requires better knowledge of historical fire and vegetation dynamics because they provide the basis for understanding potential tradeoffs in short- vs. long-term effects of management on NSO habitat.

The historical range of variability (HRV) concept (Hessburg et al., 1999; Landres et al., 1999; Brown et al., 2000; Keane et al., 2002; Wimberly, 2002; Agee, 2003a; Veblen, 2003; Nonaka and Spies, 2005; Hessburg et al., 2007) is a useful approach for describing historical fire and vegetation dynamics because it articulates characteristic responses of vegetation to disturbance and succession, thereby avoiding problematic single-date-based approaches to restoration (Choi et al., 2008). All sources of information about historical landscapes, including dendrochronology (Weisberg and Swanson, 2003), sediment core analysis (Whitlock, 1992), and aerial photo interpretation (Hessburg et al., 1999; Kennedy and Spies, 2004), have strengths and weaknesses. Key limitations of these data sources include localized extents, difficulty capturing the patchy nature of fire, limitation to recent time periods, and gaps in the chronological record. Forest landscape simulation models can be used to synthesize information gleaned from these kinds of studies to provide a view that is broader both spatially and temporally, than any singular aforementioned technique. Forest landscape simulation models that capture the dynamics of interactions of fire and vegetation (Wimberly et al., 2000; Keane et al., 2004; Scheller and Mladenoff, 2007; He, 2008) have thus been used widely to characterize the HRV and potential future range of variability (FRV) of forest conditions (Wimberly, 2002, 2004; Scheller and Mladenoff, 2005; Keane et al., 2007; Chang et al., 2008; He et al., 2008; Keane et al., 2008).

Simulation models are particularly useful for demonstrating the consequences of our assumptions about pattern–process relationships at large spatial and temporal scales, and exploring the sensitivity of model predictions to various sources of uncertainty. However, model output is only as good as the assumptions used in model specification and the data used for model parameterization. Using simulation modeling to quantify the HRV allows for the identification of thresholds where system resiliency is challenged. In addition, simulation models can be used to explore possible future scenarios that have no analog in the historical record (Seastedt et al., 2008). This type of analysis is relevant to the present issue because in the dry forests of the western U.S., climate change will likely increase the frequency and severity of fires with resulting impacts to vegetation and wildlife habitat (Westerling et al., 2006; Keane et al., 2008; U.S. Fish and Wildlife Service, 2008).

In addition to the amount of habitat available, the spatial pattern of habitat in the landscape may be an important consideration in conservation planning (Hansson et al., 1995; Rochelle et al., 1999; U.S. Fish and Wildlife Service, 2008). Whereas NSO survival is positively associated throughout its range with the amount of older forest (Noon and Blakesley, 2006) and the NSO preferentially selects older forest for nesting, foraging, and roosting (Forsman et al., 1984), the species shows variable response across its range to landscape configuration. In the southerly portion of its range, in locations where the dusky-footed woodrat (*Neotoma fuscipes*) is its primary prey, NSO fecundity has been positively associated with the amount of edge between older and the early seral stands where woodrats are present, but there is also a high survival cost of fragmentation (Carey and Peeler, 1995; Franklin et al., 2000). In the northerly portion of its range, in areas where the northern flying squirrel (*Glaucomys sabrinus*; an older forest associate) is the primary prey, understory development is important in both older and younger forest (Carey et al., 1992), and the NSO may be negatively associated with the amount of edge. The NSO selected nest locations with large patches of older forests and low amounts of forest edge in the high Cascades of southern Oregon; landscapes with extensive edges between openings and forest not suitable for nesting were less likely to be selected (Ribe et al., 1998). Thus, spatial pattern is important to the NSO. Spatial simulation models can be used to describe the characteristic spatial patterns of habitat in particular landscapes, and with information about the local prey base and other emerging knowledge about NSO demographic performance (Olson et al., 2004; Dugger et al., 2005), provide assistance to NSO conservation planning.

In this study, we characterized the historical range of variability in vegetation and fire characteristics for the Deschutes National Forest (Deschutes), a landscape in the East Cascades Province of Oregon. Much fire history research in the area has focused on specific locations (e.g. Crater Lake) or vegetation types (e.g. dry ponderosa pine), whereas we were interested in obtaining a broader view than these isolated studies portrayed individually.

Our overall goals were to better understand the HRV of the ecosystem, both in terms of vegetation and fire, and to explore model sensitivity and potential effects of future ecosystem changes to the amount and configuration of older forest. Our specific objectives were to:

(1) describe the distributions of vegetation types, late successional reserves and habitat-capable areas for the NSO in the landscape;
(2) characterize the historical range of variability in vegetation successional stages, landscape configuration, and fire risk for the landscape and its components; and
(3) assess how changes to assumptions about fire regimes and vegetation classification affect estimates of historical older forest amount and spatial pattern.

To address these objectives, we used a locally parameterized version of a forest landscape simulation model, the landscape dynamics simulator (LADS 4.6) (Wimberly et al., 2000; Wimberly, 2002; Wimberly and Kennedy, 2008). LADS combines data on fire regimes with knowledge of forest succession to generate simulations over long time periods (hundreds to thousands of years) for a given landscape. Model outputs included spatial and temporal patterns of fire frequency, fire severity, and forest successional stages. Spatial analysis of model output allowed us to characterize the range and variability of patch characteristics for older, closed-canopy forest, over the historical simulation period. Model-derived information about areas with lower historical relative risk of high severity fire (Camp et al., 1997; Meyn and Feller, 2006), was summarized to identify high priority areas for habitat protection or restoration.

2. Study area

The Deschutes is roughly 7900 km^2 in size, consisting of diverse topography and vegetation located and on the east side of the Cascade Mountains, in Oregon, USA (Fig. 1). Its young volcanic soils

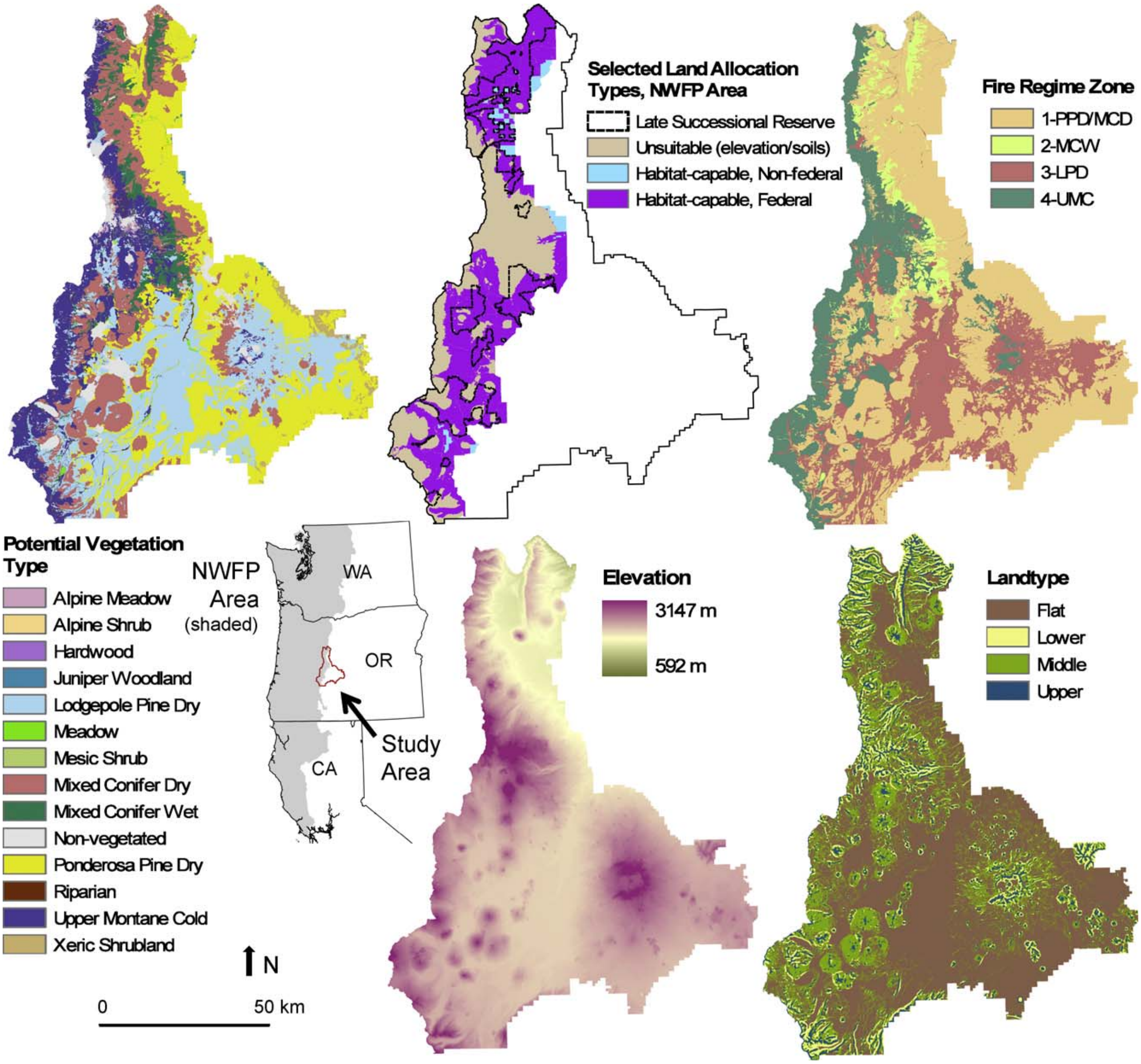

Fig. 1. Spatially explicit attributes of the Deschutes National Forest in the Pacific Northwest, USA, used in landscape fire succession modeling and analysis: potential vegetation types, land allocation types, fire regime zones; elevations, and land types. Scale bar pertains to attribute figures. Inset map shows NWFP Area extent in Oregon, Washington, and California.

have moderate water-holding capacity, poor heat transfer, and coarse textures (Volland, 1985). Elevations range from 593 to 3147 m. The dry continental climate is highly variable across the study area, with mean monthly temperatures ranging from −13 to 29 °C and mean annual precipitation (primarily winter snow) from 261 to 2875 mm (PRISM Group, Oregon State University, http://www.prismclimate.org, 1971–2000 data, June 2006).

Vegetation types are linked to the spatial distribution of soils, topography, and temperature, with water the primary factor limiting plant growth (Volland, 1985; Franklin and Dyrness, 1988). Potential vegetation types (and representative species) prevailing in the eastern zone and at lower elevations (Fig. 1) include dry ponderosa pine (*Pinus ponderosa*) forest, dry mixed conifer forest (a mixture of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), white fir (*Abies concolor*), lodgepole pine (*Pinus contorta*), and incense cedar (*Libocedrus decurrens*)), western juniper (*Juniperus occidentalis*) woodland, and xeric shrubland dominated by big sagebrush (*Artemisia tridentata*). Wetter forest types occur higher on the slopes of the volcanic peaks and include wet mixed conifer forest (ponderosa pine, white fir, Douglas-fir, Shasta red fir (*Abies magnifica shastensis*), Engelmann spruce (*Picea engelmannii*), and western larch (*Larix occidentalis*)), and upper montane cold forest (∼>1525 m) (subalpine fir (*Abies lasiocarpa*), mountain hemlock (*Tsuga mertensiana*), whitebark pine (*Pinus albicaulis*), western white pine (*Pinus monticola*), Shasta red fir, and lodgepole pine) (Fig. 1) (Volland, 1985). Dominant trees tend to be long-lived (ponderosa pine, ca. 300–600 years; Douglas-fir, 400–700; mountain hemlock, 700+; whitebark pine, 500–1000), with exceptions (lodgepole pine, 80–100; subalpine fir, 200–300) (Burns and Honkala, 1990).

The area has a management history of logging with preferential removal of large Ponderosa pine and Douglas-fir trees, grazing, and post-Euro-American settlement fire suppression (circa 1900s). These management activities have altered forest structure, composition, and dynamics (Everett et al., 1997; Hessburg et al., 2005; Hemstrom et al., 2007). Historical fires had high (>75% aboveground vegetation killed), moderate (25–75% killed) and low (<25% killed) severity effects (Agee, 1993). A mixed severity fire regime resulted where there was high spatial variability in the distribution of fire severities. This type of fire regime was also characteristic of other mixed conifer forests in the Pacific Northwest (Hessburg et al., 2007).

3. Methods

3.1. LADS model description

LADS combines spatially explicit fire ignition, spread, and effects subroutines with a state-and-transition model of forest succession to simulate forest landscape dynamics. The model was originally parameterized for forests in western Oregon (Wimberly et al., 2000; Wimberly, 2002; Nonaka and Spies, 2005; Nonaka et al., 2007). We recently updated the model to simulate fire and forest dynamics in low, high, and mixed-severity fire regimes in dry forests of the Pacific Northwest, U.S. (Wimberly and Kennedy, 2008). The current version of LADS simulates variability in fire spread and effects as a function of fuels, forest structure, site moisture, and topography. Forest succession subroutines depict multiple pathways of forest development, with transitions among successional stages resulting from overstory tree growth, fire-induced tree mortality, and establishment of shade-tolerant cohorts in the absence of fire (Wimberly and Kennedy, 2008).

3.2. Model parameterization and sensitivity analysis

Driving variables used in the LADS model for the Deschutes included digital maps of four fire regimes, four landtypes, 14 potential vegetation types (PVTs), elevation, and slope. These spatial data were represented in raster format with a 30 m grid cell size (Fig. 1). A single prevailing wind direction (270°) was specified for all simulations. A set of successional pathways and successional stage-specific responses to high, moderate, and low severity fires described vegetation dynamics.

Preliminary sources for spatial vegetation data included a plant association guide (Volland, 1985) and a plant association groups map (unpublished data) developed by Deschutes National Forest personnel. Successional stages were defined for each of eight PVTs: (hardwood (HW), juniper woodland (JW), lodgepole pine dry (LPD), mixed conifer dry (MCD), mixed conifer wet (MCW), ponderosa pine dry (PPD), upper montane cold (UMC), xeric shrubland (XS) (Fig. 1; Table 1). Each successional stage depicted a unique forest cover-structure combination. Successional stage definitions, transition parameters, and fire severity modifiers for each cover-structure combination (Table 1) were developed from a synthesis of the regional literature (McNeil and Zobel, 1980; Bork, 1985; Morrow, 1985; Franklin and Dyrness, 1988; Simon, 1991; Agee, 1993, 1998, 2003a; Camp et al., 1997; Foster, 1998; Heyerdayhl et al., 2001; Wright and Agee, 2004; Youngblood et al., 2004; Siderius and Murray, 2005; Spies et al., 2006; Hemstrom et al., 2007; Hessburg et al., 2007) and from existing state-and-transition models. Succession was modeled as transitions from one successional stage to another at predetermined time increments (Table 1). If a fire ignited or burned though a grid cell, vegetation could transition to a new post-disturbance successional stage. The probability distribution of fire severities (low, moderate, or high) differed for each successional stage within a PVT. Fire severity determined the post-disturbance transition: e.g., a moderate severity fire in a late mature closed canopy successional stage cell would open the canopy, but not remove large trees or set back the age of the grid cell, whereas a high severity fire would reset the grid cell to the early successional grass/forb stage with age zero (see Wimberly and Kennedy (2008) for more details).

We distinguished four fire regime zones in the Deschutes (Fig. 1; Table 2). We based these primarily on major differences in vegetation, after testing numerous other approaches such as purely elevational gradients, and a single fire regime zone. Potential vegetation types are often used to describe disturbance effects on the environment (Hall, 1998; Hessburg and Agee, 2003). Fire regime zone 1 was dominated by the ponderosa pine dry and mixed conifer dry PVTs, (low severity/high frequency) Zone 2 by mixed conifer wet (low-moderate severity, low-moderate frequency), Zone 3 by lodgepole pine dry (moderate severity/moderate frequency), and Zone 4 by upper montane cold (high severity/low frequency (Agee, 1993, 1998, 2003a). Fire size distributions for each fire regime were derived from the literature and a Deschutes map of historical fires (1908–2003).

Four landtypes (Fig. 1) described flat areas, lower slopes/valley bottoms, middle slopes, and upper slopes/ridgetops, and differed in their effects on fire initiation and spread. For example, fires were more likely to ignite on upper slopes/ridgetops, and spread faster, whereas valley bottoms/lower slopes were less likely to be ignited, and fires spread more slowly. Fires were also sensitive to slope, spreading faster in upslope than in downslope directions.

3.3. Landscape analysis

We simulated historical landscape dynamics on the Deschutes for 10,000 years; this followed an initialization period of 2000 years which overwrote starting conditions where particular successional stages had been assigned for each PVT. In this approach, thousands of years are simulated to capture the range of possible landscape realizations (Wimberly, 2002; Keane et al., 2003; Nonaka and Spies, 2005). We summarized model output (maps and tabular data) at 100-year intervals. Vegetation summaries included the landscape-level distributions for each successional stage of each potential vegetation type and time since fire. Fire regime summaries included the proportion of fires that were low, moderate, and high severity, and the mean fire return interval.

Because the spatial pattern of habitat is an important consideration for NSO conservation planning, we described the spatial structure for older forest and other successional stages in the simulated historical landscape by summarizing the distribution over time of six landscape metrics. Total class area (CA) and proportion of the landscape occupied by a patch type (PLAND) indicated the patch type's relative dominance in the landscape. Patch density (PD), mean patch area (AREA_MN), and largest patch index (LPI; percent of the landscape occupied by the largest patch of a given type) and edge density (ED) measured the sizes and shapes of each type of patch. These metrics have been used in other recent HRV modeling research (Keane et al., 2002; Wimberly, 2002) and we selected them since they are relatively straightforward to interpret and characterize different components of landscape configuration. We computed these metrics using FRAGSTATS v. 3.3 (McGarigal et al., 2002) for each landscape summary from the baseline historical and sensitivity analysis simulations.

We defined 'older forest' as that which contained late mature or old overstory age classes (>76.2 cm diameter at breast height) and any level of canopy closure (open/medium/closed) based on the desired characteristics from the NSO recovery plan (Table 1). "Habitat-capable areas" (HCAs) were defined as those areas that have the potential to support NSO populations based on an elevational isocline that varied throughout the NWFP area (Davis and Lint, 2005), and were consistent with the NSO recovery plan. Prior research has indicated much LSR area is not potentially suitable habitat for the NSO; in the Oregon Eastern Cascades physiographic province, just 54% of reserved land is considered to

Table 1
Baseline parameters for successional pathways for major central Oregon forest potential vegetation types.

PVT	Code	Overstory age class	Canopy closure	Min. age	Max. age	Max. TSFIRE	PHS	PMS
MCD	GF	Grass/forb	Early successional	0	10	10	0.375	0.375
	SS	Seedling/sapling	Early successional	11	25	15	0.375	0.375
	PO	Pole	Open	26	60	30	0.075	0.075
	YO	Young	Open	61	90	30	0.0375	0.0375
	EMO	Early mature	Open	91	120	30	0.015	0.015
	LMO	Late mature	Open	121	180	30	0.0075	0.0075
	OO	Old	Open	181	NA	30	0.0075	0.0075
	PM	Pole	Medium	26	60	40	0.375	0.375
	YM	Young	Medium	61	90	40	0.15	0.6
	EMM	Early mature	Medium	91	120	40	0.15	0.6
	LMM	Late mature	Medium	121	180	40	0.0375	0.7125
	OM	Old	Medium	181	NA	40	0.0375	0.7125
	PC	Pole	Closed	26	70	NA	0.7125	0.0375
	YC	Young	Closed	71	110	NA	0.675	0.075
	EMC	Early mature	Closed	111	150	NA	0.6	0.15
	LMC	Late mature	Closed	151	230	NA	0.6	0.15
	OC	Old	Closed	231	NA	NA	0.55	0.15
LPD	GF	Grass/forb	Early successional	0	10	10	0.5	1
	SS	Seedling/sapling	Early successional	11	30	20	0.5	1
	PO	Pole	Open	31	60	40	0.5	1
	YO	Young	Open	61	140	40	0.4	1
	PC	Pole	Closed	31	60	NA	0.7	1
	YC	Young	Closed	61	NA	NA	0.6	1
MCW	GF	Grass/forb	Early successional	0	10	10	0.3	1
	SS	Seedling/sapling	Early successional	11	25	15	0.3	1
	PO	Pole	Open	26	60	30	0.2	0.075
	YO	Young	Open	61	90	30	0.125	0.0375
	EMO	Early mature	Open	91	120	30	0.075	0.015
	LMO	Late mature	Open	121	180	30	0.035	0.0075
	OO	Old	Open	181	NA	30	0.035	0.0075
	PM	Pole	Medium	26	60	40	0.3	1
	YM	Young	Medium	61	90	40	0.25	1
	EMM	Early mature	Medium	91	120	40	0.2	1
	LMM	Late mature	Medium	121	180	40	0.175	1
	OM	Old	Medium	181	NA	40	0.45	1
	PC	Pole	Closed	26	70	NA	0.45	1
	YC	Young	Closed	71	110	NA	0.45	1
	EMC	Early mature	Closed	111	150	NA	0.4	1
	LMC	Late mature	Closed	151	230	NA	0.35	1
	OC	Old	Closed	231	NA	NA	0.35	1
PPD	GF	Grass/forb	Early successional	0	10	10	0.5	1
	SS	Seedling/sapling	Early successional	11	35	25	0.5	1
	PO	Pole	Open	36	80	40	0.15	0
	YO	Young	Open	81	125	40	0.075	0
	EMO	Early mature	Open	126	170	40	0.0375	0
	LMO	Late mature	Open	171	260	40	0.015	0
	OO	Old	Open	261	NA	40	0.015	0
	PM	Pole	Medium	36	80	NA	0.5	1
	YM	Young	Medium	81	125	NA	0.4	1
	EMM	Early mature	Medium	126	170	NA	0.2	1
	LMM	Late mature	Medium	171	260	NA	0.1	1
	OM	Old	Medium	261	NA	NA	0.05	1
UMC	GF	Grass/forb	Early successional	0	10	10	0.25	1
	SS	Seedling/sapling	Early successional	11	40	30	0.35	1
	PO	Pole	Open	26	60	30	0.4	1
	YO	Young	Open	61	90	30	0.35	1
	EMO	Early mature	Open	91	120	30	0.3	1
	LMO	Late mature	Open	121	180	30	0.25	1
	PC	Pole	Closed	26	70	NA	0.45	1
	YC	Young	Closed	71	110	NA	0.4	1
	EMC	Early mature	Closed	111	150	NA	0.4	1
	LMC	Late mature	Closed	151	230	NA	0.45	1

MCD: mixed conifer dry; LPD: lodgepole pine dry; MCW: mixed conifer wet; PPD: ponderosa pine dry; UMC: upper montane cold; Min. age: starting stand age for that overstory class; Max. age: stand age at which transition to the next overstory age class occurs; Max. TSFIRE: time since fire at which transition to the next canopy closure class occurs; PHS: probability that a fire will be high severity; PMS: probability that a fire will be moderate severity. PMS = 1 indicates no probability of low severity fire. PMS = 0 indicates no probability of moderate severity fire; all fires that are not high severity will be low severity.

be habitat-capable (Davis and Lint, 2005). Therefore, we assessed fire and vegetation characteristics of the HCAs and NWFP-related land allocations (LSR, NWFP area, Non-LSR NWFP area, Non-NWFP Deschutes) in the PVT map we developed and LADS output (fire and vegetation) maps in conjunction with relevant USFS GIS grids (Davis and Lint, 2005) Regional Ecosystem Office GIS data, http://www.reo.gov/gis/data/gisdata/).

We also conducted a sensitivity analysis (Wimberly, 2002; Wimberly and Kennedy, 2008) to assess how changes in model representation of fire regimes or vegetation classification schemes

Table 2
Fire parameters used in the dry forest landscape baseline (historical) and fire regime sensitivity analysis simulations of the landscape age-class dynamics simulator (LADS). FRZ is fire regime zone.

Parameter	Description	Baseline scenario	Sensitivity scenarios	
			–	+
NFR1	Natural fire rotation for FRZ 1 (years)	15	12	18
NFR2	Natural fire rotation for FRZ 2 (years)	100	80	120
NFR3	Natural fire rotation for FRZ 3 (years)	60	48	72
NFR4	Natural fire rotation for FRZ 4 (years)	200	160	240
MFS1	Mean fire size for FRZ 1 (km^2)	750	600	900
MFS2	Mean fire size for FRZ 2 (km^2)	350	280	420
MFS3	Mean fire size for FRZ 3 (km^2)	200	160	240
MFS4	Mean fire size for FRZ 4 (km^2)	2000	1600	2400
SDFS1	SD of fire size for FRZ 1 (km^2)	375	300	450
SDFS2	SD of fire size for FRZ 2 (km^2)	175	140	210
SDFS3	SD of fire size for FRZ 3 (km^2)	100	80	120
SDFS4	SD of fire size for FRZ 4 (km^2)	1000	800	1200
CHS1	Climate severity modifier for high severity fires for FRZ1 (see text)	1	0.8	1.2
CHS2	Climate severity modifier for high severity fires for FRZ2 (see text)	1	0.8	1.2
CHS3	Climate severity modifier for high severity fires for FRZ3 (see text)	1	0.8	1.2
CHS4	Climate severity modifier for high severity fires for FRZ4 (see text)	1	0.8	1.2
CMS1	Climate severity modifier for moderate severity fires for FRZ1 (see text)	1	0.8	1.2
CMS2	Climate severity modifier for moderate severity fires for FRZ2 (see text)	1	0.8	1.2
CMS3	Climate severity modifier for moderate severity fires for FRZ3 (see text)	1	0.8	1.2
CMS4	Climate severity modifier for moderate severity fires for FRZ4 (see text)	1	0.8	1.2

might affect the amount of older forest and simulated landscape patterns. Each of these sensitivity analysis simulations consisted of a 1000-year simulation period following a 1000-year initialization phase, with landscape summaries computed at 10-year intervals. We compared the mean values of the various landscape indices relative to the baseline (historical) simulation.

To explore the sensitivity of model outputs to changing fire regimes, we varied by ±20% the baseline (historical) values for natural fire rotation (NFR), mean fire size (MFS), standard deviation of fire size (SDFS), climate severity modifier for high severity fires (CHS), and climate severity modifier for moderate-severity fires (CMS) (Table 2). The CHS and CMS parameters effectively function as 'tuning knobs' that allow fire severity for all successional stages to be modified as a function of temporal variability in climate. We modified values for all four fire regime zones simultaneously to examine broad-regional effects of climate change rather than more localized responses. We modified SDFS simultaneously with MFS, to reflect the strong correlation between these two parameters. Wimberly (2002) had determined that LADS model results were not highly sensitive to changes in the wind parameter, so we held that variable constant for all model runs.

Variability in the criteria used to classify older forest has been noted as an ongoing potentially problematic issue since NWFP implementation (Moeur et al., 2005). To test how assumptions about forest successional stage classification may lead to different predictions of available older forest, we compared LADS simulations of patch characteristics and landscape dynamics under the historical fire regime for two vegetation classification schemes. The 'Fixed-size' scheme classified older forest by the presence of large and very large trees and single- or multistoried canopies (Table 1). The 'PVT-adjusted size' scheme classified older forest with tree size indexed by potential vegetation type. Except for the inclusion of small ('young' in Table 1) trees in the lodgepole pine PVT, most of the 'PVT-adjusted size' additions to older forest were in minor vegetation types such as hardwoods and riparian areas. We ran the model on the finest classification elements, which did not vary according to classification scheme. Then, we grouped individual PVT-specific successional stages into generalized successional classes (early successional to older forest according to 'fixed size' or 'PVT-adjusted size' breaks) prior to conducting further analyses.

4. Results

4.1. The distribution of potential vegetation types

Five potential vegetation types comprised most of the NWFP area within the Deschutes. In rank order, they were: mixed conifer dry (MCD), upper montane cold (UMC), mixed conifer wet (MCW), lodgepole pine dry (LPD), and ponderosa pine dry (PPD) (Table 3), with MCD and UMC predominating at 32 and 31%, respectively, in the NWFP area. LSRs and habitat-capable areas (HCAs) had even higher proportions of MCD and less UMC, reflecting the association of UMC with higher elevation sites (Table 3).

Although numerous vegetation types occurred in the LSRs and HCAs, not all of them would be expected to provide habitat for the NSO. For example, although it comprises roughly 14% of the NWFP area of the Deschutes, lodgepole pine dry forest would neither meet the medium-to-closed canopy nor late mature or old overstory age class requirement. In fact, about 16% of the HCAs, and 9% of LSRs, was occupied by PVTs lacking the potential to provide older forest (Tables 1 and 3). Additionally, the ponderosa pine dry PVT is generally considered to be too open-canopied to provide NSO habitat (U.S. Fish and Wildlife Service, 2008), removing an additional ~10% from the potentially suitable land base for NSO in both LSRs and HCAs. This type of condition further restricts the ability of land managers to provide habitat for the NSO and other late successional, closed canopy forest-associated species in these dry forest landscapes.

4.2. Historical range of variability of forest conditions

The simulated landscape spatial configurations of forest cover-structure classes varied over time. Old overstory and early successional classes were the most abundant and were of similar amounts, with old overstories occupying a median of 26% of the area (range 25–27%), and early successional occupying 25% (23–26%). Young forest and pole stages were next in rank, with median abundances of 16% and 15%, respectively (15–17% and 14–16%), over the simulation period. Late mature overstories occupied a median 10% of the landscape (9–10%), and early mature, 4% (4–5%). About 4% of the landscape was non-vegetated (water/rock/ice).

Table 3
Potential vegetation types as percent of land allocation area within Deschutes National Forest, Oregon, and total land area in each allocation.

	Total NWFP	LSR NWFP	Non-LSR NWFP	HCA
Alpine meadow	0.47	0.01	0.65	0.00
Alpine shrub	0.02	0.05	0.01	0.03
Hardwood	0.03	0.08	0.01	0.05
Juniper woodland	0.00	0.00	0.00	0.00
Lodgepole pine dry	10.07	6.25	11.53	13.76
Meadow	0.49	0.14	0.62	0.03
Mesic shrub	0.63	1.03	0.47	0.75
Mixed conifer dry	32.34	50.24	25.48	43.51
Mixed conifer wet	11.36	16.67	9.32	15.12
Non-vegetated	6.74	1.77	8.64	0.84
Ponderosa pine dry	6.26	11.17	4.38	9.67
Riparian	0.43	0.00	0.59	0.28
Upper montane cold	31.15	12.56	38.28	15.94
Xeric shrublands	0.01	0.04	0.00	0.02
Total area (ha)	327,437	90,795	236,642	183,864

NWFP: Northwest Forest Plan Area; LSR: Late Successional Reserve; HCA: Habitat-Capable Area for Northern Spotted Owls.

These and all other simulation results derived from the fixed-size successional scheme, unless otherwise noted.

Old overstories had the largest patches, with a mean largest patch index (LPI) of 6% of the landscape vs. an LPI of 2% for early successional and 1% for young patches (Fig. 2). Early successional patches had the highest edge densities, followed in rank order by old, pole, young, late mature, and early mature types. Densities of old overstory patches were, on average, at most about half that of the other cover-structure classes at 13 patches/km^2; young and late mature patches had the highest densities (39 patches/km^2).

Successional stages had fine-grained variability in spatial pattern, with adjacent individual 30 m pixels commonly in different stages of development that reflected the heterogeneous nature of fire spread (Fig. 3). At coarser resolutions particular successional conditions tended to prevail, with individual pixels of various successional stages occurring within these larger patches (Fig. 3). This circumstance occurred regardless of potential vegetation type, simulation year or land allocation type.

Changing the vegetation succession classification scheme affected patch metrics (Fig. 2). Classifying vegetation using the fixed-size successional scheme resulted in lower patch densities and lower edge densities for late mature and old overstory patches. Likewise, using the fixed-size scheme led to greater densities of pole and young patches, and larger mean patch areas for early seral and young patches than the PVT-adjusted-size scheme. The density of old overstory patches was lower and mean area for old overstory patches was higher for the fixed-size scheme. On the other hand, the largest old overstory patch tended to be larger using the PVT-adjusted size scheme, and there were several positive outliers, or very large patches, using this scheme.

4.3. Older forest characteristics

'Older forest', which consisted of both late mature and old overstory stages, was about 35% of the simulated historical

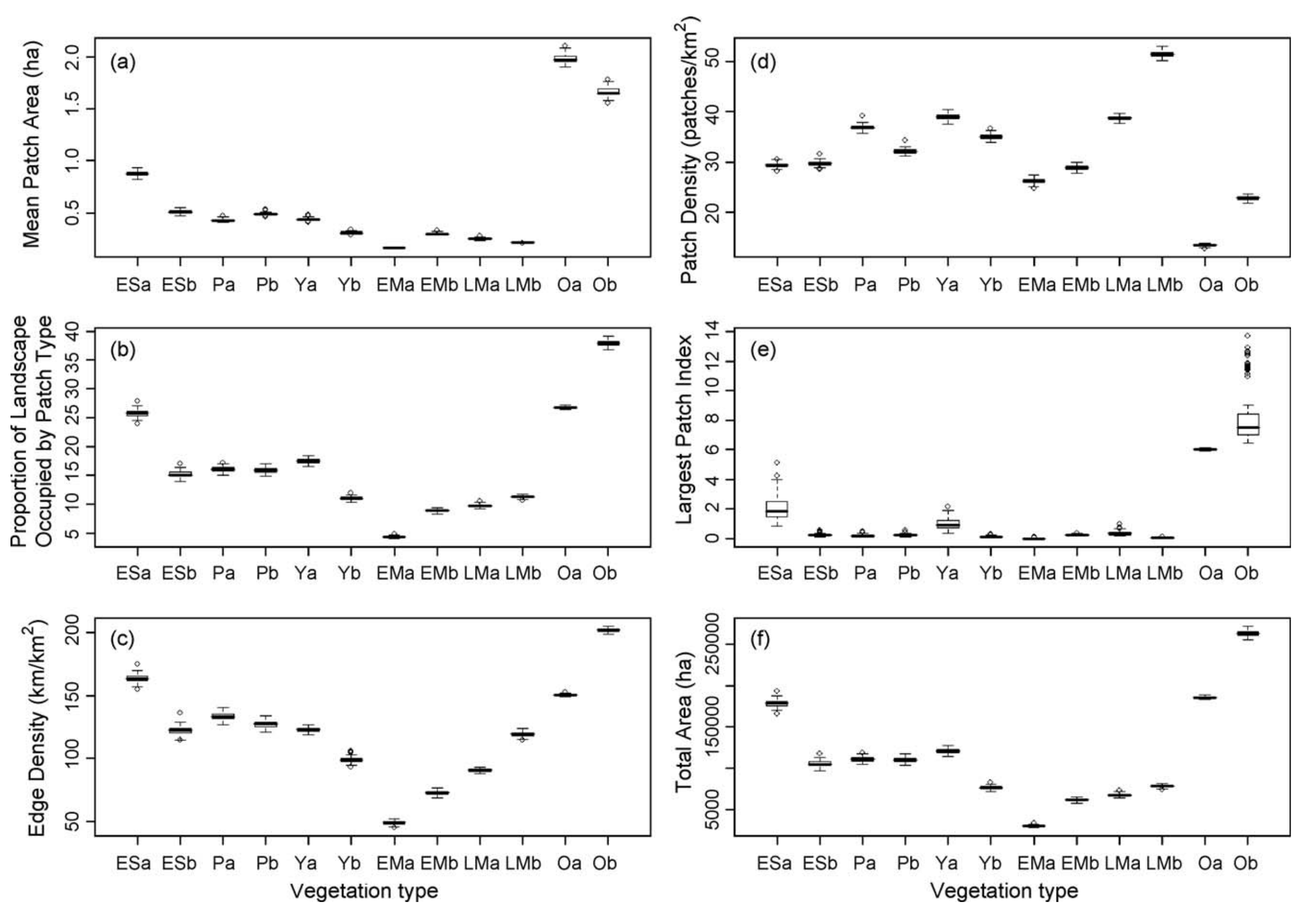

Fig. 2. Box-and-whisker plots of patch characteristics for fixed-size and PVT-adjusted size classification schemes, summarizing 100-year-interval maps of forest vegetation from a 10,000 year simulation of historical landscape dynamics of a dry forest landscape in the Pacific Northwest, USA. (a) Mean patch area; (b) proportion of landscape occupied by patch type; (c) edge density; (d) patch density; (e) largest patch index; and (f) total area occupied by patch type. Vegetation type codes: ES = early successional; P = pole; Y = young; EM = early mature; LM = late mature; O = old. Code suffix 'a' = fixed-size successional scheme; 'b' = PVT-adjusted size scheme.

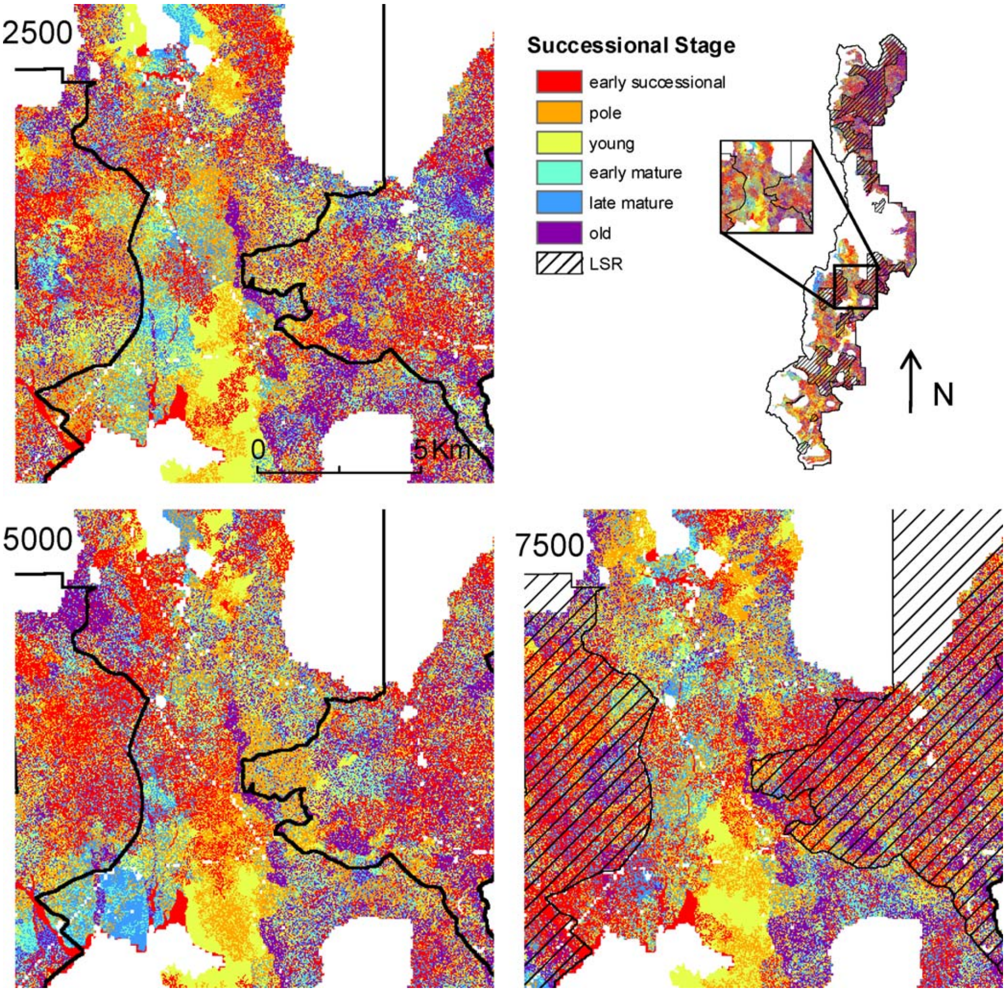

Fig. 3. Detail views of successional stages from the simulation of historical fire and vegetation dynamics for habitat-capable areas of the Deschutes National Forest for years 2,500, 5,000, and 7,500, depicting fine-grained spatial heterogeneity of fire effects, areas within LSRs incapable of producing northern spotted owl habitat, and areas outside LSRs capable of producing owl habitat.

landscape, on average. This total was comprised of 26% in open canopy forest and 9% in multilayer canopy medium or closed canopy forest. There was modest variability in older forest amount, with medium-to-closed canopy stages having higher interannual variation than open canopy (Fig. 4); probably because both moderate and low severity fire would serve to open a closed canopy. Most older forest in the Deschutes was ponderosa pine dry (~18% of landscape), with an open canopy. About 6% was the mixed conifer dry open canopy type (Fig. 4).

The upper montane cold and ponderosa pine dry PVTs had the greatest amounts of older forest with medium-to-closed canopy structure of all PVTs in the simulated historical Deschutes landscape (Fig. 4). In part, this result reflected the greater abundance of these vegetation types in the landscape than the

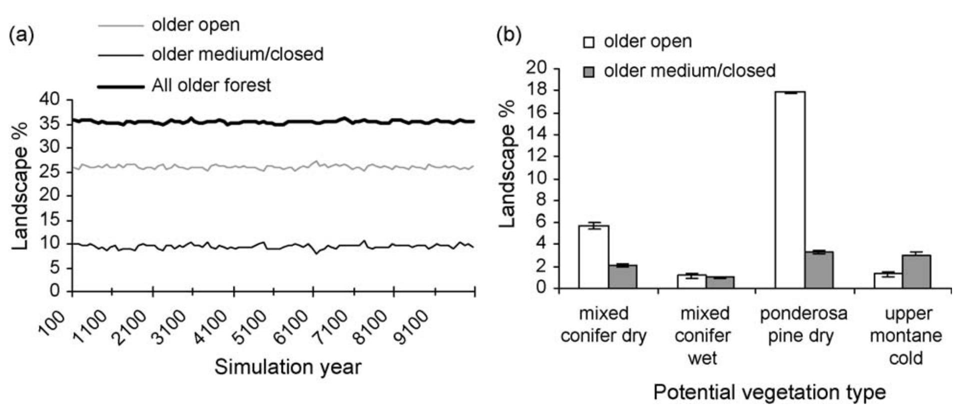

Fig. 4. Simulated historical mean amount and variability in older forest with open and medium-to-closed canopy structure in a dry forest landscape of the Pacific Northwest, USA for a 10,000 year simulation period. (a) Time series of older forest structural types; and (b) Mean amount for the four potential vegetation types capable of producing late mature and old overstory age classes under the fixed-age successional scheme. Error bars in (b) are SDs.

other two old-forest-capable PVTs. However, whereas these two PVTs provided about 67% of the landscape's older medium-to-closed canopy forest, they occupied only about 25% of the habitat-capable area. Thus, much of the older medium-to-closed canopy forest was outside the area that would be suitable for NSO habitat: at elevations that were too high (i.e., some upper montane cold) or in places beyond the borders of the NWFP area and outside the current range of the NSO (i.e., some ponderosa pine dry).

The spatial attributes of older forest patches with medium-to-closed canopies also differed from those of their open counterparts (Fig. 5). These were fewer and smaller than the open patches. Combining these into a single older forest patch type ('all') resulted in larger patches, but also a greater amount of edge per unit area. Small (>1 ha) patches of medium-to-closed canopy older forest tended to be situated adjacent to or within somewhat larger (circa. 1.75–2.25 ha) open older forest patches.

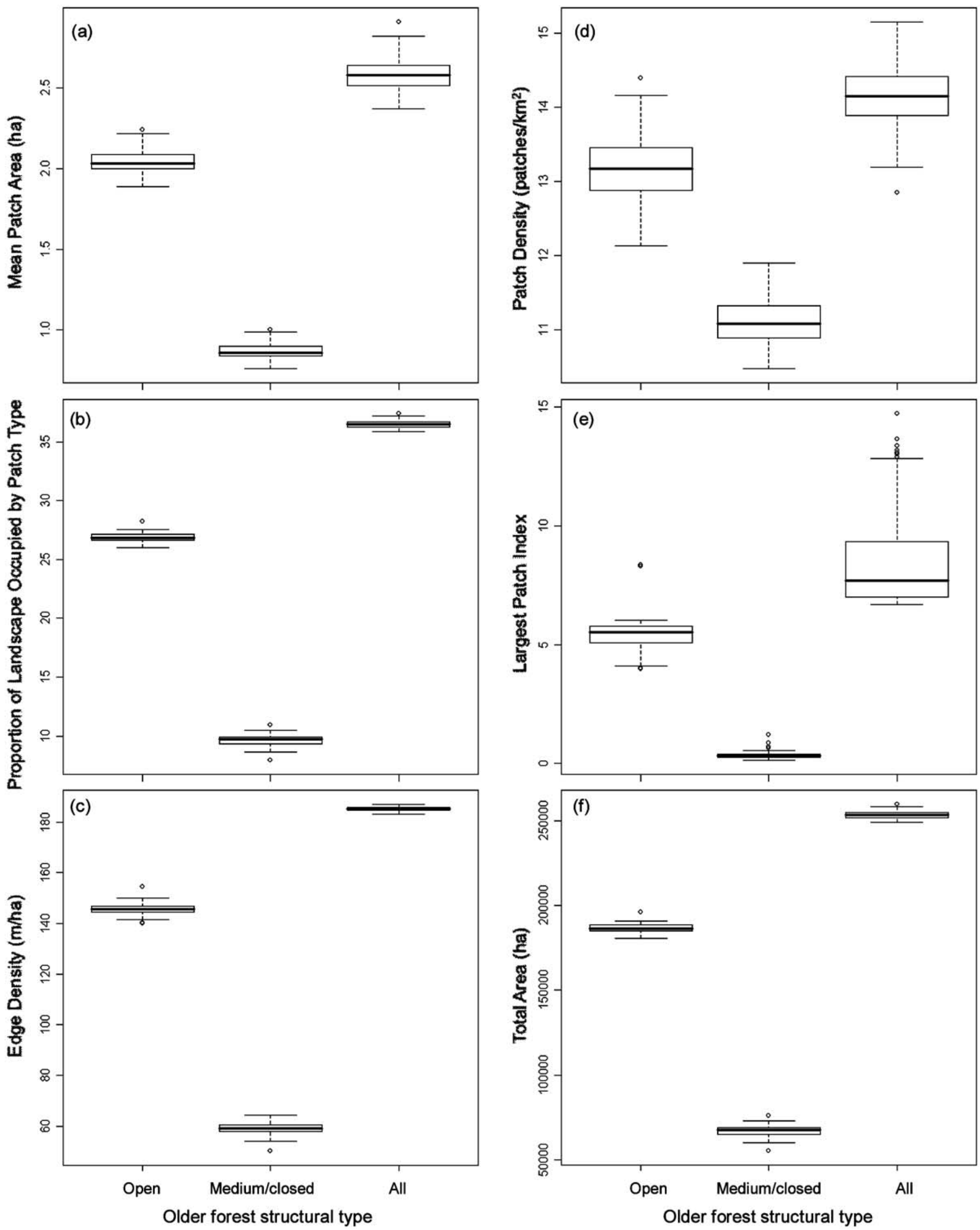

Fig. 5. Box-and-whisker plots of patch characteristics for open, medium/closed, and all older forest structural types, summarizing 100-year-interval maps of forest vegetation from a 10,000 year simulation of historical landscape dynamics of a dry forest landscape in the Pacific Northwest, USA. (a) Mean patch area, (b) proportion of landscape occupied by patch type, (c) edge density, (d) patch density, (e) largest patch index, and (f) total area occupied by patch type.

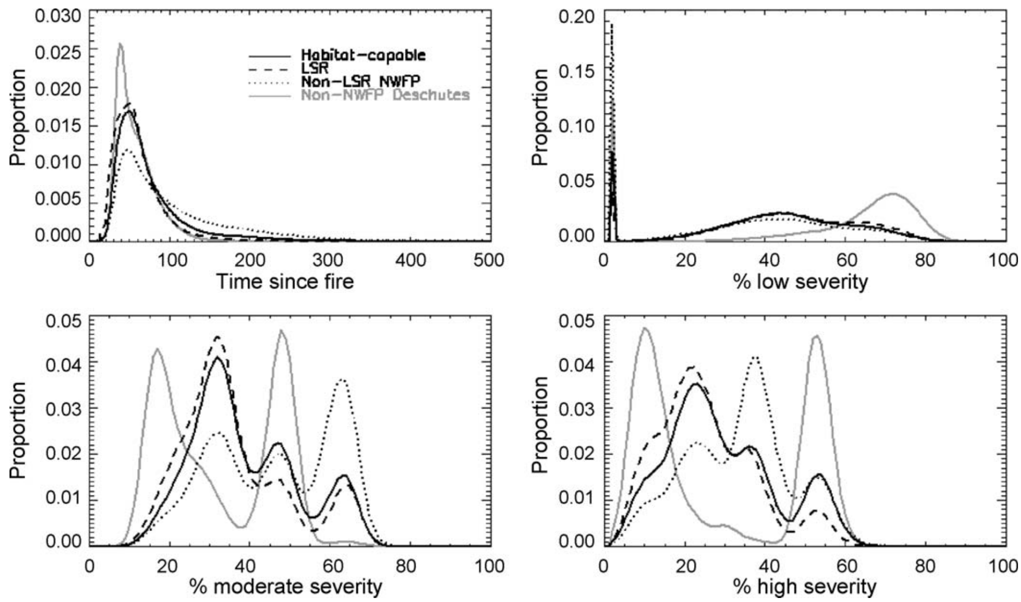

Fig. 6. Proportional frequency distributions of fire regime characteristics by Northern Spotted Owl-related land allocation type, from a simulation of historical fire and vegetation dynamics in the Deschutes National Forest, a dry forest landscape in the western USA: time since fire; % low severity fire; % moderate severity fire; and % high severity fire.

Table 4
Mean (median) likelihood of occurrence of fire of various severities given the incidence of fire, and time since fire across the landscape by land allocation type.

	HCA	LSR NWFP	Non-LSR NWFP	Non-NWFP Deschutes	Deschutes
% Low severity fire	33 (38)	40 (43)	21 (0)	39 (55)	35 (39)
% Moderate severity fire	39 (35)	36 (33)	46 (47)	33 (29)	36 (35)
% High severity fire	29 (27)	25 (24)	34 (35)	30 (19)	30 (27)
Years since fire	76 (61)	62 (54)	107 (79)	60 (52)	77 (57)

4.4. Spatial and temporal patterns of fire and vegetation

HCAs and LSRs had similar frequency distributions for time since fire across their respective areas through the simulation period. They tended to burn with frequencies slightly higher than the entire NWFP area, and slightly lower than the non-NWFP area of the Deschutes (Figs. 6 and 7; Table 4). With respect to the incidence of high and moderate severity fire, LSRs and HCAs had unimodal distributions, the non-reserve areas of the NWFP had unimodal distributions with peaks at higher percentage values, and the non-NWFP Deschutes area had bimodal distributions. In the non-NWFP Deschutes, some areas experienced very little high severity fire, whereas in others high severity fire predominated. Most low severity fires tended to occur in the non-NWFP Deschutes.

4.5. Effects of changing fire regimes on older forest

Changing fire severities resulted in the greatest shifts in amount of older forest (Fig. 8), vs. changing fire sizes or frequencies. A 20% change in mean fire severity across the four fire regime types resulted in about a 4% change in older forest, relative to the

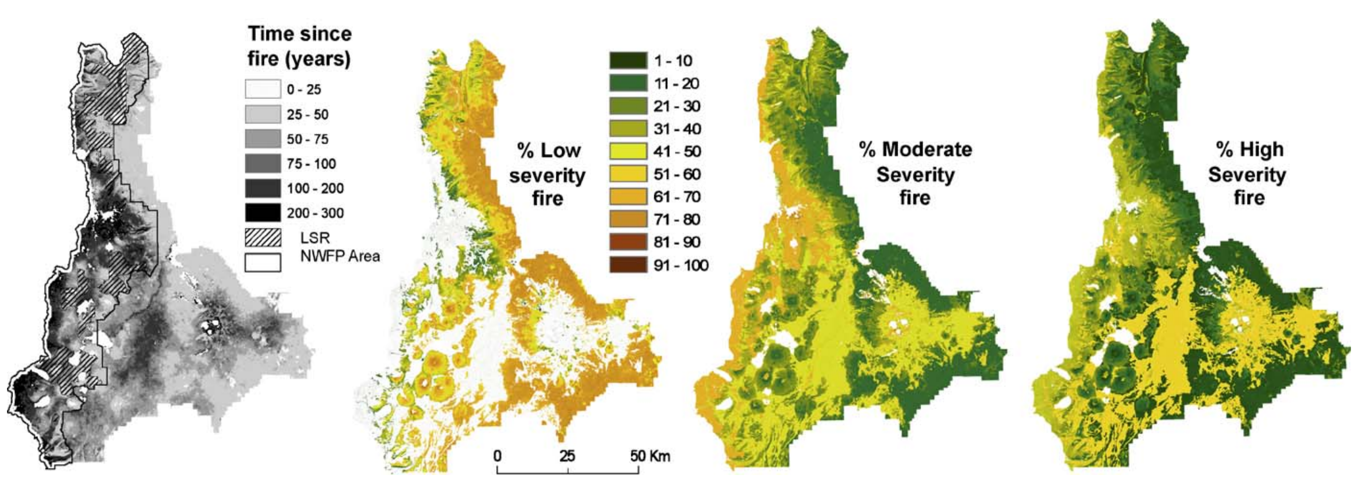

Fig. 7. Mapped characteristics of historical fire regimes over a 10,000 year simulation period for the Deschutes National Forest, USA. (a) Mean time since fire, (b) percent of the time fires were low severity, (c) percent of the time fires were moderate severity, and (d) percent of the time fires were high severity.

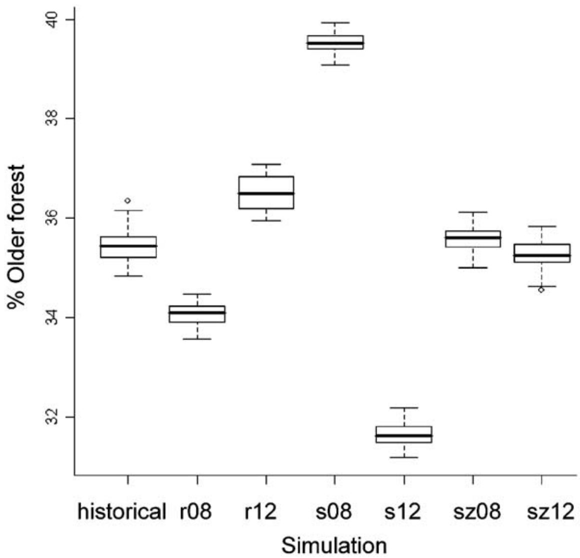

Fig. 8. Box-and-whisker plots of percent older forest from baseline (historical) and sensitivity analysis fire and vegetation dynamics simulations for Deschutes National Forest, USA. *X*-axis letters indicate modified parameters: *r* = natural fire rotation; *s* = climate severity modifier; *sz* = mean fire size. Number that follows indicates multiplier (without decimal) used on base parameter setting; e.g., if base *r* = 15 years, then *r*08 = 12 years.

baseline HRV scenario. Changing the mean and standard deviation of fire size by $\pm$20% for all fire regime types did not lead to significant differences in the percent older forest relative to the HRV simulation. Increasing the frequency of fire by 20% across the four fire regime types had a greater effect on the percent older forest than decreasing the frequency of fire by 20%, but the median values for both were within two percentage points of the amount of older forest produced under the baseline simulation of historical conditions.

5. Discussion

The Deschutes National Forest landscape was characterized historically by a fire regime that consisted of a mixture of low, moderate, and high severity fires, with moderate severity fires being most common, on average. Simulated fire regimes consisted of many small, low-to-moderate severity fires occurring at high frequencies, and few larger, less frequent, moderate and high severity fires. These were both promoted by and resulted in vegetation spatial patterns that were similarly complex (see, for example, Figs. 3 and 7). This finding is generally consistent with retrospective analyses of dry forest landscapes in eastern Washington using aerial photography (Hessburg et al., 1999; Hessburg et al., 2000). A study of mixed conifer forest in three ecological subregions in eastern Oregon and Washington also found that a mixed severity fire regime (20.1–69.9% canopy mortality) dominated. That study found that the proportion of mixed severity fire was about 67% of all fires for moist forest and 52% for dry forest in the subregion associated with the Deschutes (Hessburg et al., 2007); they did not assess patch spatial pattern. Likewise, a study of fire scars in two ponderosa pine/Douglas-fir-dominated landscapes in the eastern Cascades of Washington indicated that overlapping fires created a complex mosaic of different fire histories, typical of spatially heterogeneous landscapes (Everett et al., 2000). Whereas that study described fire history polygons for two subwatersheds, the present study described spatial pattern and dynamics of multiple vegetation types of interest and associated fire characteristics across a large landscape.

Our research highlights the importance of understanding within-landscape spatial pattern and temporal variability of landscape-wide historical fire-related metrics. This is even more relevant if they are used as reference points for land management planning for federally listed species such as the threatened NSO. Understanding how fire shaped past landscape mosaics prior to fire suppression and logging has been noted as important to developing silvicultural practices that might benefit the NSO in dry forest landscapes (Franklin et al., 2000).

The results of our study suggest that the characteristics of the landscape matrix varied by vegetation type, with large (circa. 2.0 ha) patches of open older ponderosa pine forest being characteristic of the historical fire regime at the scale of the entire landscape, but with smaller (circa. 0.75 ha) patches of older, medium/closed canopy forest in both the ponderosa and other forest types. The historical landscape consisted of both open and closed canopied older forest types, and also contained smaller patches of younger forest types. This finding is consistent with previous assessments of westside forests (Wimberly, 2002). This suggests that landscape patterns composed of a large number of small patches embedded in a smaller number of larger patches can be generated by a broad range of natural fire regimes.

We did not find large differences in the amount and spatial characteristics of older forest if we changed the classification scheme to include a slightly expanded definition of older forest conditions. This indicates that the fundamental conclusions with respect to vegetation dynamics may not be sensitive to minor changes in the definition of older forest. Instead, uncertainty about historical fire regimes and the future effects of climate change and land management on fire regimes are likely to have a greater influence on assessment of older forest habitat.

The Eastern Cascades physiographic provinces have only modest amounts of NSO habitat-capable land, relative to the other provinces in the Northwest Forest Plan area (Davis and Lint, 2005). Within the LSRs of these provinces, this habitat-capable land is irregularly distributed; some areas of LSRs are not capable of producing NSO habitat, and some LSRs are situated completely outside the habitat-capable areas (c.f. Fig. 1). Additional habitat-capable areas lie outside the LSRs. Our analyses indicated that LSRs and HCAs were very similar in their historical fire regime characteristics and potential to produce older forests. Thus, if a goal is to increase the land base for the NSO, managers may want to conserve some amount of the non-LSR HCAs to augment the LSRs. Our simulation modeling results provide guidelines about historical patch sizes and amounts of forest successional stages and older forest by PVT that can be used as a starting point for developing management strategies.

With respect to the restoration of older forest conditions in dry forests, our simulations indicated that historically, the Deschutes had the capacity to maintain about 35% of its area as older forest, with about 9% having closed canopy structure potentially amenable as NSO habitat. Current land allocations, modified landscape functions, management directives, or future disturbances may not allow for this amount of older forest. Numerous changes are likely in the dry forests of the western U.S. in coming decades from climate change and population increases in the region. These include changes in fire regimes, geographic shifts in tree species distributions, introduction of novel invasive species, pests and pathogens, changes to the timing and amount of moisture availability, changes in site productivity, and continued development with resulting land-use changes in the wildland–urban interface. Our analyses of fire severity, frequency, and size indicated that changes in fire regimes resulting from climate shifts or land management practices will modify the amount and spatial pattern of older forest. Further analyses will be required to explore potential implications of combined factors such as the interaction of fire with tree species migration and loss, increased insect infestations via climatically related changes in insect demographics, potential tradeoffs of increased atmospheric CO_2 on plant productivity in combination with decreased water availability, and barred owl effects. Evaluating tradeoffs of proposed management scenarios on fire risk in dry forests and implications for conservation planning is an area of increasing research (Wilson and Baker, 1998; Roloff et al., 2005; Ager et al., 2007) and quantitative and probabilistic risk assessment theory development (Kerns and Ager, 2007). The present study provides a framework for the assessment of potential future scenarios in this risk assessment context: model outputs describing the future range of variability can be contrasted with the HRV characteristics described here to provide quantitative, component-level measures of departure.

Recent fires in the eastern Cascades of Oregon illustrate the direction future fire regime changes may take. The B&B complex fires of 2003 burned 367 km^2, 268 km^2 of which was within the Deschutes National Forest. In this area, according to Forest Service reports, 33% of the fire area burned at low severity, 19% at moderate severity, and 46% at high severity, with 51% at high severity in the LSRs (USDA FS, B&B Fire Recovery Project Final Environmental Impact Statement). These fires resulted in substantial losses of older forest (Spies et al., 2006). The landscape burned with a greater proportion of higher severity fire than would have been expected historically based on the results of our study, regardless of land allocation type; for LSRs, we estimated approximately 25% of fires would be high severity under historical conditions. Recent conditions likely resulted at least in part from increased fuel loads from fire suppression, a prevailing circumstance in the inland Northwestern U.S. (Hessburg et al., 2005). Our simulation results indicate that increasing the incidence of high severity fire will cause greater reductions in older forest habitat than changes in fire size or frequency. The current LSR network needs to be assessed for the potential to maintain or restore historical quantities of older closed canopy forest without augmentation. Land areas outside the LSRs that are within the HCAs, and that have older forest structure or could be managed to provide it within a few decades, may provide opportunities for increasing the amount of older forests relative to the present landscape condition. Further research is needed to determine the specific land management strategies that would be most effective at sustaining older forest and providing NSO habitat in dry forests of the inland Pacific Northwest in appropriate configurations. These assessments will need to examine tradeoffs between the maintenance of older forests and other management goals. In particular, they will need to address the risk of older forest loss from wildfire and other environmental changes.

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